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EXPERIMENTAL STUDIES UPON HYDROMEDUSAE.

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IN connection with previous work on regeneration the problem of animal grafting was repeatedly suggested by many phenomena associated with that work, and during the summer of 1898 a series of experiments was undertaken at the Marine Biological Laboratory and carried on through the months of July and August.

It is a pleasure in this connection to acknowledge many courtesies extended by the director, Prof. C. O. Whitman, and valuable suggestions from Dr. Jacques Loeb, during the progress of the work. The following paper aims simply to present a résumé of methods and results, deferring speculative considerations which might be suggested by any of the phenomena involved.

I. *Material.*

This was restricted to two sorts of organisms, Hydroids and Medusae. Of Hydroids an almost unlimited amount and of many genera and species were available and easily obtained from the waters about the docks of the U. S. Fish Commission, from the rocks and fucus in the harbor and adjacent waters. It was obtained fresh every morning and experiments were made only upon it within a few hours. The genera used in the experiments were Eudendrium, Pennaria, Parypha, and a few of the Campanularidae.

Of Medusae only one species was available in sufficient abundance and size for experimentation, namely, *Gonionemus vertens*, a Medusa occurring in considerable numbers in the "eel pond," a small body of water adjacent to the laboratory and communicating with the waters of the harbor by a very

narrow inlet. As this Medusa endures artificial conditions with considerable ease for days and even weeks, it lends itself readily to such experiments. Its size also, varying from 2 or 3 mm. to as many cm., is also a factor of convenience, though a larger species would prove desirable in some operations. Its activity during at least three months also facilitates extended experiments.

II. *Methods.*

In grafting the Hydroids, the stems were cut into fragments varying from 5 to 10 mm. in length, and usually taken from the younger and fresher portions of the stem. Successful unions were made from older portions but in much smaller proportions, and requiring much longer time. The hydranths were excised, since the motion of the body and tentacles would invariably disturb the contact of the specimens. Having pre-

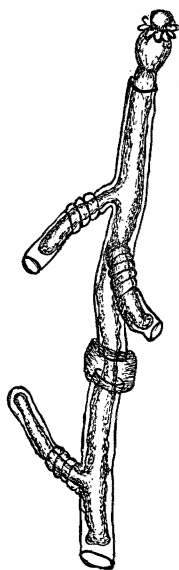


FIG. 1.

pared suitable sections, they were brought into contact in watch-glasses, or small petri dishes, of perfectly fresh sea water, and retained in position by small bits of lead shaved freshly from thin sheets. Bits of platinum wire would have been better, though it was not available at the time, and little appreciable difficulty was had with the lead. The water was changed on the specimens daily.

With the Medusae the task was a much more difficult one, for while the power of spontaneous movement had been largely eliminated by emarginating the bell and thus removing the marginal nerve ring, and thus the centers of spontaneity, the contractility had not been destroyed, and for a time great difficulty was found in retaining the parts in even contact. And in this connection I desire to correct a partial error in my previous paper on "Regeneration,"¹ where I had failed to recognize the paralyzing effects of such emargination, a fact due to failure

¹ *Zoölogical Bulletin*, I, p. 29.

to remove sufficient of the margin. If the least portion was left, or even a portion quite near the margin, automaticity was retained, but by removing carefully and completely some 2 or 3 mm. of the bell-margin I was able to confirm quite fully the experiment of Romanes¹ on Scyphomedusae.

After various expedients had failed, resort was had to bits of rather fine shoemaker's bristles, cut into proper lengths. These were thrust through the gelatinous portions of the Medusae in such directions as would serve to fairly secure the desired contact of the surfaces to be united. An inspection of the several figures will give the best idea of how this was secured. Cf. Figs. 8 and 9. But at best the method was only partially successful. It may be mentioned in this connection that one of the difficulties attending these experiments was the danger of deleterious contamination involved in the whole of

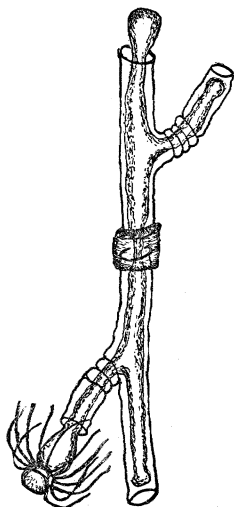


FIG. 2.

the operations from Bacteria and parasitic Infusoria invading the water and impeding or destroying the experiments. This was much more noticeable in experiments on Medusae than on Hydroids, a fact due in part, certainly, to the promptness with which the latter reacted in regeneration of tissues as compared with the former. Notwithstanding, it is rather remarkable that so small a proportion in either case suffered, since no *special* pains were taken in the way of critically guarding against contamination beyond the more ordinary provisions of clean glassware and instruments. To maintain a fairly equable temperature during unusually hot days, the covered vessels containing the specimens were set under the running water taps of the laboratory.

¹ Jellyfishes, etc., p. 27 *et seq.*

III. *Grafting.*

Hydroids. — The work upon Hydroids was restricted chiefly to species of *Eudendrium*, *Pennaria*, and *Parypha*, though a few experiments were tried upon *Campanularians*. Upon the latter the results were almost entirely *negative*, though for this no apparent cause was ascertained. The experiments were not of sufficient numbers, nor of sufficiently varied conditions, to warrant any conclusions as to the incapacity of these to regenerate or coalesce. Time was not adequate to extend the

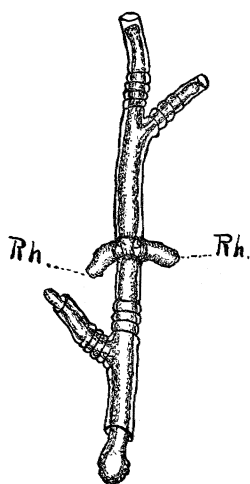


FIG. 3.

attention to this group which might have resulted more favorably. Again, the relatively small size of the members of this group available was a further embarrassment to successful experimentation. However, neither of these is offered as sufficient account of the negative character of the experiments. Indeed, the work of Davenport ('94) on *Obelia* is strongly affirmative, at least so far as regeneration is concerned.

Experiments upon species of the genera named were specially successful. While of course in all such work a large number of failures must result, yet when the difficulties of manipulation and the artificial conditions necessary are considered, this is not strange.

While no mathematical estimates were made as to the ratio of successful experiments, I think it may be safely said that at least 20 per cent of all were successful. It need hardly be pointed out that results varied materially in both the time necessary, and the degree of perfection, in the coalescences. This will be noted in detail in connection with the several experiments described.

A comparison of the several figures will perhaps indicate in general better than words the methods and results. Cf. Figs. 1-6.

The union between sections of the same species was usually quite perfect within from eighteen to thirty-six hours. A

delicate sheath of perisarc secreted over the ends was the first indication of special activity and regeneration. This usually occurred at any wounded point. It became specially marked at the points of contact of the grafted specimens. The first effect of the sectioning of the specimens preparatory to their being placed in contact was a pronounced contraction of the coenosarc within the tubular perisarc, and the closure of the cut ends of the enteric cavity. This was usually, however, soon followed by an outgrowth till the coenosarc of the two specimens came into contact, when the secretion of the extra perisarc proceeded as a joint operation, though sometimes by a single one, if its activity and response were the more prompt. Cf. Figs. 1 and 2.

Following this the contact of the two became more intimate, the healed ends united with each other, fusion being followed by the absorption of the terminal portions and the consequent confluence of the enteric channels and their contents.

In the experiments no apparent difference was noticeable as to anything like polarity, the parts uniting orally, aborally, or otherwise, with equal freedom and promptness. With species of *Eudendrium* and *Pennaria* this was demonstrated with absolute certainty, the directions of the branches making any mistaking impossible. Cf. Figs. 2-4.

In these species the sexes are distinct, and experiments in grafting specimens of the opposite sexes were quite as prompt and perfect as otherwise. There would seem, therefore, to be not only no definite differences of polarity as seems to be the case in *Hydra*, but no sexual difference in so far as regenerative or coalescence capacity is concerned. It remains to note results as to grafting different species. With none of these are the distinctions sufficiently clear to warrant positive con-

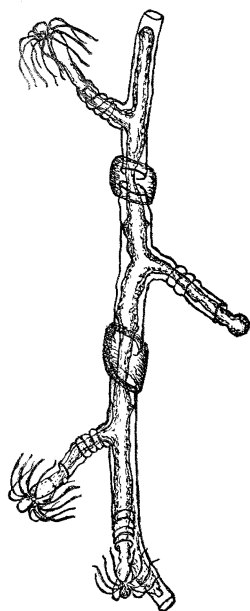


FIG. 4.

clusions. Of *Pennaria*, only one species was available, and the same was true of *Parypha*. Of the species of *Eudendrium* there have been several indicated, but their distinctness is to my mind open to serious doubt.

If the distinctness of Agassiz's species of *E. dispar* and *ramosum* is to be maintained, then the grafting of these has been as clearly established as that of the different sexes. It would not be strange should closely allied; though definitely distinct, species be found to coalesce in these organisms, for such has been long known among plants, and shown for animals by the recent experiments of Born ('96), Crampton ('97), Harrison ('98), and others. But so far as I am aware it has not hitherto been demonstrated for the Hydroids; indeed, most of such efforts have been negative in results.



FIG. 5.

As to the coalescence between specimens of different genera, the experiments seem to be conclusive and wholly negative. Out of a considerable series, while there were indications of temporary union, in no case did it become conclusively permanent. The most favorable indications were upon *Eudendrium* and *Pennaria*, Hydroids of very similar size, structure, and habit; but after repeated experiments under different conditions the results were as already indicated. In Fig. 6 it will be noted that the usual secretion of perisarc at the points of contact has been deposited, and apparently by the coöperation of both sections; still at no time were there evidences of organic union of the coenosarc, and later this was distinctly withdrawn, and the sections continued an independent existence, each producing new hydranths, though

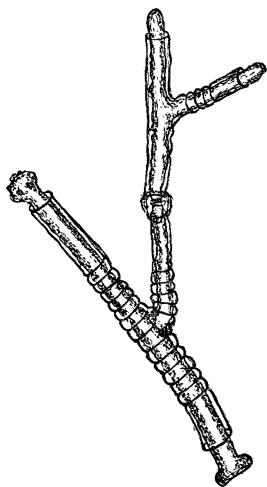


FIG. 6.

in the case of *Eudendrium* they continued rudimentary in the specimen figured.

IV. *Medusae.*

Experiments upon Medusae were restricted to *Gonionemus vertens*, being the only species available in sufficient numbers, and capable of adaptation to the artificial condition necessitated by the nature of the work. This Medusa is found in great numbers, though only in a limited locality adjacent to the Marine Laboratory, and lives readily for several days, or even weeks, in table aquaria, if reasonable precautions be taken to keep the water fresh and supply suitable food.

While the experiments were quite extensive and various, aiming at first to ascertain the trend of resultants, no attempt will be made in this connection to describe them in any con-



FIG. 7.

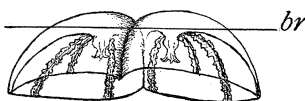


FIG. 8.

siderable detail, but rather to call attention to a few of the more conspicuous of them, and to indicate something of their probable significance.

Fig. 7 will afford a good idea of the general features of the Medusa with the entire margin of the bell and its organs excised, preparatory to any contact experiments.

In Fig. 8 are shown two Medusae from which portions have been removed, the larger part of each being brought into contact and retained by the bristle, *br.*, passing through the body. In some instances two or three bristles were passed through in different planes, thus giving greater stability of contact.

Parts of various sizes and from different regions were similarly grafted, and with usually similar results. The time required for union differed greatly in experiments conducted under exactly the same conditions and care. In some cases complete union had taken place within twenty-four hours, while in others it only occurred after several days. It should be noted, however, that when once coalescence had begun it usually went forward with comparatively great rapidity.

In Fig. 9 is shown the coalescence of two Medusae by their oval margins. This was usually the most easily performed of any of the experiments upon the Medusae, and union was rather more prompt if any difference was noticeable. As will be seen from the figure, fusion was not entire in this case, a

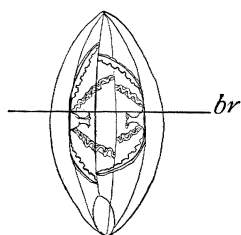


FIG. 9.

small mouth-like opening remaining on one side through which aëration of the interior was made possible, and by means of which by contraction the united individuals were able to move about in the water. It should be noted in this connection that upon stimulation coördinated movements were produced, and in a few instances even apparently spontaneous movements were clearly recognized. I have said that this action was *apparently* spontaneous. It is not impossible, of course, that some extraneous stimulus might have been involved, but, if so, it was wholly beyond any ordinary physical detection, and was distinctly recognized by several persons to whom it was pointed out.

In these experiments, in a few cases, the specimens united completely throughout the entire margin, but with the result that the specimen died within a comparatively short time, presumably from inability to secure aëration of the portions where metabolism was most active and aëration most imperative.

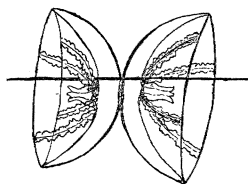


FIG. 10.

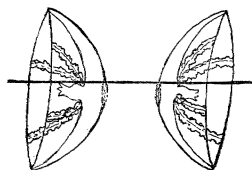


FIG. 11.

Figs. 10 and 11 show a method of aboral grafting made upon a considerable number of specimens, but uniformly without permanent success. As will be noted in Fig. 11, the points of contact were slightly scarified, or in some cases portions excised with sharp scissors, in order to favor coalescence of

the surfaces, but after a few hours the specimens would almost invariably have drawn apart by some sort of creeping movements, probably aided in part by the prehensile character of the manubrium, and usually one or both finally extracting the bristle entirely. I am not able to suggest any satisfactory explanation of the negative character of this experiment. Whether regenerative tissue is wanting on this area, or whether some intrinsic repugnance to such fusion be the cause or occasion, or whether some cause wholly undetected was present, seems a matter of doubt. There would seem to be no *a priori* reason why this particular experiment should not find as ready a response as those already described. The inverted position could hardly be assigned, for specimens in similarly inverted aspects readily united by the margins, as indicated in Fig. 12.

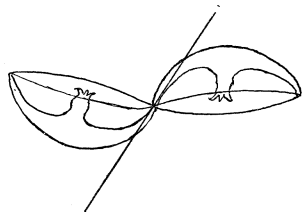


FIG. 12.

In Figs. 13-16 is shown a phenomenon which appeared in connection with the series of experiments quite incidentally, and of which I shall undertake no particular explanation, and yet which is one of the most novel and interesting of the entire series.

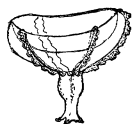


FIG. 13.

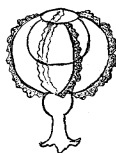


FIG. 14.

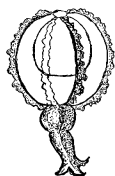


FIG. 15.

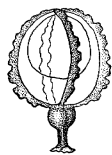


FIG. 16.

In certain aboral grafts, similar to those already described in Fig. 10, a single specimen was found with the bell somewhat evaginated, as in Fig. 13. During the following days, July 27 and 28, it passed successively through the phases represented in Figs. 14, 15, and 16, becoming permanently united in the completely evaginated form of Fig. 16, in which condition it continued to live and even take particles of food, though it showed no evidences of growth, beyond a distension of the gastric pouch due to the engulfed food. Finally, on August 3 the specimen died during the very sultry night, and was found the

following morning in a partially disintegrated condition, a result due in part to the unusual temperature, and perhaps in part to overfeeding.

A series of experiments were undertaken by which to secure, if possible, by artificial means other inversions of a similar sort, and though various expedients were adopted by which to facilitate such, they gave no permanent results.

The phenomenon of eversion in the Medusae of *Obelia* and other Hydroids in their young or newly discharged condition is quite well known, but it continues for a brief time only, and with no disposition toward permanence so far as I have known.

Of course the classical experiments of Trembley (1744), Nussbaum ('87, etc.), and others upon *Hydra* are too well known for special comment, and at first sight might be thought to be analogous to that now under consideration ; but a moment's reflection will suffice to show that it is only so in a very general way. For example, there is no inversion of the relative position of ectoderm and endoderm, since the lining of the bell, outer surface of the manubrium, etc., is ectodermal. The enclosed cavity of the everted specimen served no new function in its changed condition, nor did the outer layer in its new relations. That any change in the histological characters would be induced may therefore be considered very unlikely since the change of relative position, while considerable, is yet not such as would necessitate any change of function. Nevertheless the fact is an interesting one, and apparently quite unique. At one time, just about the completion of union of the inverted margins, a decided papilla-like bud appeared at the aboral area which presented some resemblance to a second manubrium, but this soon after was absorbed entirely, and was probably only the elevation due to the approximation of the margins preparatory to final union.

V. *Regeneration and Heteromorphosis.*

In connection with the foregoing experiments occasion was taken to repeat some of my earlier experiments on regeneration and to extend them somewhat. At an earlier point in

this paper I have indicated an error in the former paper, as to the paralysis of the Medusa following the complete removal of the marginal portion of the bell. I desire, moreover, to express more definitely than appears in the earlier paper, though it was clearly implied at several points, the fact that in all those experiments there does not appear to be any actual increase of mass, or growth of the body as a whole, but that in all the regenerative activity it was evidently at the expense of other portions of the body proper. This would naturally follow in most cases, since in producing a new manubrium, or new tentacles, or in the grafting experiments, the animal was practically incapacitated for obtaining food, and under the artificial conditions of the experiment could hardly have been suf-

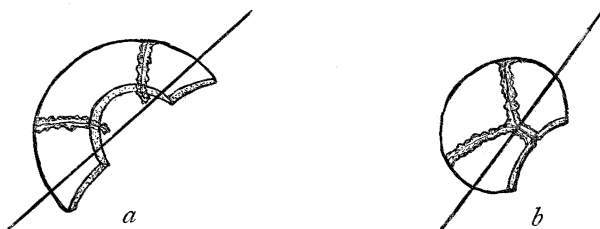


FIG. 17.

ficiently fed to make evident any growth. In many cases a very evident decrease in size was apparent in the progress of the experiment. Indeed, in many cases manubrium, velum, tentacles, etc., continued to live for weeks accompanied by a gradual decrease in the body mass, till it finally became wholly consumed, after which the organs gradually disintegrated.

In all essentials the later experiments confirm those earlier made. Further attempts were made to put specimens under such conditions as would render difficult any mere contraction or approximation of the surfaces. Figs. 17 and 18 will show two out of a considerable number and variety of the experiments. In these the portions of the body were set in their relative positions by bristles in such a way that only continued contractions of considerable vigor would be able to change them. But within forty-eight hours the results indicated in the several figures had taken place, the stereotypic form of body assumed,

and without indication of specific regenerative growth and absolutely no hint at heteromorphism in the slightest way.

Figs. 19 and 20 show experiments designed to further test the regeneration of the manubrium. The operation of removing the organ was made on August 4. As will be seen in the case of Fig. 19, about three-quarters of the animal were excised, leaving one chymiferous canal fairly complete, and a mere remnant of a second, the whole of the manubrium hav-

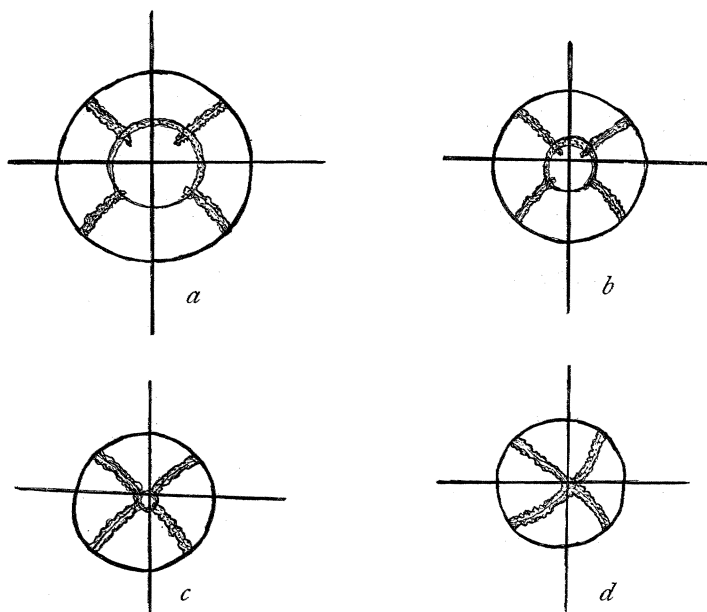


FIG. 18.

ing been removed, as indicated by the line of the cut, *a-b*. In Fig. 20 a wedge-shaped piece, about one-fourth the body mass, including the manubrium, one entire canal and the central portions of the other three, as indicated, was excised.

On August 5 the cut margins in each case had approximated each other and were evidently uniting. On August 7 the union was complete and the Medusae were swimming quite freely and naturally. On August 9 the first indications of a new manubrium were apparent, and in approximately the normal position. Its color and texture clearly indicated its forma-

tion as a new outgrowth, there being only the slightest traces of pigment present. The growth was quite gradual, and not until about August 14 had it become fully formed and functional.

In each case there had also been regenerated additional radial canals, as indicated in the figures. These appeared in connection with the lines of union, and were not at first

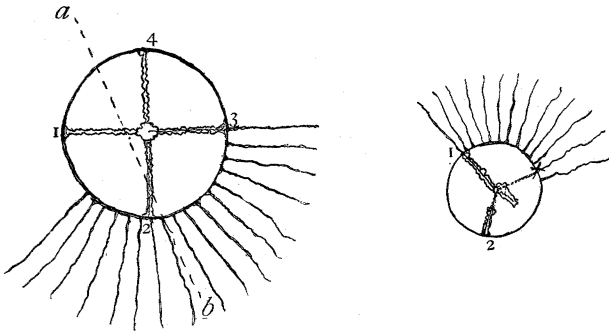


FIG. 19.

suspected as canals. Later the deposition of pigment along their course pointed strongly to the conclusion that they were canals, though whether yet functional I am not able to say.

In none of my experiments has there been any clear confirmation of the results and conclusions of Bickford ('94) that in Hydroid regeneration the polyp, tentacles, etc., are produced

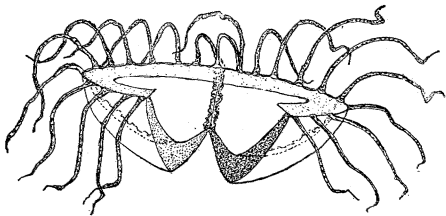


FIG. 20.

simply by a "transformation of the tissues of the stem"—that is, that the tentacles are formed by a sort of longitudinal cleavage of the coenosarc, and a remolding of it directly, without any tissue changes. In cases where there is only a recasting of a portion of the body into the *form* of the original, as in the case of a Medusa divided into sections, where each

part assumes the typical shape of the whole, being only different in *size*, this is of course clear. But from an inspection of Fig. 1 it will be evident that the tentacles are regenerated by a process of budding and growth exactly as in Hydra. The same was even more evident in the regeneration of tentacles, manubria, etc., in the Medusae. In every case they originate as minute buds, and become functional only after a considerable period of growth.

Whether additional tissue is formed from "*a few undifferentiated cells*," a sort of reserve embryonic tissue, may indeed be doubtful. Still, that there is *growth* in the ordinary histogenic sense must be evident in these cases as truly as in that of the regeneration of the tail or limb of the newt. And, indeed, it hardly seems to be more than a verbal quibble whether it be by one or *both* processes. For in either case it simply implies the presence in these organisms of cells or tissues possessing the capacity, shared in common with embryonic or undifferentiated tissues, of reparation.

VI. *Historical.*

Experimental work on the Hydrozoa may be said to date from the classical researches of Trembley, published in 1744, upon species of Hydra. He divided specimens into pieces of various sizes and shapes, and from various portions of the body, securing entire polyps from each.

He turned polyps inside out and had them live and thrive for months. He also grafted portions of one upon another with equal facility and success.

These researches were later repeated by Baker, who, while confirming some of Trembley's experiments, was not able to do so for all of them. Similar results were had by Rösel von Rosenhoff in 1755, who in addition claimed to have secured entire polyps from fragments of tentacles.

In 1878 Engelmann again repeated Trembley's experiments, and with results very similar to those of von Rosenhoff.

Marshall in 1882 was not able to secure successful grafting or eversion, but regeneration of polyps from portions of ten-

tacles, the body of the tentacle becoming the body of the polyp, and in turn forming new tentacles.

Nussbaum in 1887 and 1890 successfully everted specimens and described the process by which the body layers righted themselves. He secured no regeneration from detached tentacles.

Ischikawa in 1889 experimented upon eversion of Hydras successfully and described the process by which the layers readjusted themselves, differing in some respects from the account of Nussbaum.

In 1895 and 1898 Wetzel grafted specimens and secured union between portions of same species; but while bits of a different polarity united, the distinctness of polarity was only exceptionally modified. He secured only temporary unions of portions of different species.

Miss Peebles in 1897 undertook the determination of the smallest portions of Hydra capable of regeneration.

Rand in 1898 worked out interesting results on the "Regulation" of regeneration in Hydra.

Comparatively little has been done of an experimental nature upon Hydroids.

Loeb in 1891 carried on an extensive series of experiments on regeneration and heteromorphosis among Hydroids, chiefly of the genera *Antennularia*, *Eudendrium*, and *Tubularia*, with the object of determining as far as possible the external conditions and causes which affect life and growth. Light and gravitation were shown to have a profound influence in determining many of the phenomena.

In 1892 Miss Bickford conducted experiments on *Tubularia tenella*, confirming in many points the work of Loeb.

Davenport in 1894 conducted regenerative experiments upon *Obelia commisuralis*, with a view to determining the distribution of generative or embryonic tissue in various regions of the Hydroid.

The contribution of the present writer to the general subject in 1897 has already been cited.

Driesch in 1897 reviewed the work of Loeb and Bickford on *Tubularia*.

Summary and Conclusions.

1. Tubularian Hydroids readily react to experiments directed toward regeneration or grafting.
2. They exhibit in most cases striking illustrations of heteromorphosis.
3. They show no marked polarity, readily coalescing in either oral or aboral relations.
4. They show no sex differentiation of tissues limiting the process of grafting.
5. Closely allied species may be intergrafted.
6. Different genera have not been successfully grafted.
7. Hydromedusae respond to regenerative and grafting experiments with almost equal readiness.
8. No definite aboral grafting of Medusae has been successfully made.
9. Medusae show throughout a sharp polar orientation.
10. No heteromorphic results have been shown among Medusae.

SYRACUSE UNIVERSITY, June, 1899.

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